BOTANICAL MUSEUM LEAFLETS
HARVARD UNIVERSITY

AMBRIDGE, MASSACHUSETTS, OCTOBER 5, 1938 VOL. 6, NO. 8

RESUPINATION AS A DIAGNOSTIC CHARACTER IN THE ORCHIDACEAE WITH SPECIAL REFERENCE TO MALAXIS MONOPHYLLOS

BY
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TO OUR EYES there is something quite proper in the usual position of the labellum of an orchid flower. I suppose our demands for pleasing symmetry go as far as this, that the weightier parts should be the lowermost. (cf. plate of *Cypripedium parviflorum* opposite p. 146) Yet in the bulk of orchid species the labellum owes its satisfying position to a twist of 180 degrees in the ovary or pedicel, proof enough that it is in reality the uppermost member of the perianth, rendered the lowermost by some vagary of nature, or shall we say, by a sympathetic physiological response to the behavior of those food-seeking insects which accomplish pollination.

In the bud of an orchid flower the labellum is adaxial; in other words, it is adjacent to the axis of the inflorescence. If there were not any change in the pedicel or ovary up to and during anthesis, the labellum would remain adaxial. In orchids which have many-flowered racemes it is possible to observe the progressive turning of the buds as the pedicel and ovary twist, until in the expanded flower the labellum, by more or less pronounced curvature of the ovary near the base of the flower, be-

CYPRIPEDIUM PARVIFLORUM var. PUBESCENS
An example of resupination.

comes the lowermost member of the perianth and is adjacent to the subtending floral bract. This is very clearly and beautifully exhibited by *Goodyera pubescens.* (cf. plate opposite p. 150) In this species the raceme develops in such a manner that it attains considerable length before anthesis and the basal flowers begin to expand only after the inflorescence is about to burst into full bloom. Consequently throughout the raceme there is a protracted period of juvenility. This being so, it is possible before a single flower has opened to trace in the buds every stage of ovarian torsion and curvature between the adaxial position of the labellum and complete resupination of the perianth.

In many genera there may be torsion in the rachis as well as in the pedicel or in the ovarian tissues. Torsion may be clockwise or counter-clockwise as is true of *Spiranthes gracilis*; the inflorescence then takes on the aspect of spirality. In these cases torsion has occurred in the ovary, pedicel and rachis. In many species of orchids there may be a pronounced drooping of the raceme and the flowers then become resupinate.

Whatever influences are at work, the orchid flower is designated as being resupinate when the labellum is the lowermost segment of the perianth. This condition was defined by Lee in 1765 as follows: "A Resupination; which is, when the upper Lip of the Corolla looks toward the Ground, and the under Lip towards Heaven." John Lindley, in his Vegetable Kingdom, third edition (1853) p. 173, described the orchid flower as being "very often resupinate in consequence of a twist in the ovary." And Vines, in his translation of Sachs' textbook of botany implied that resupination is bound up with torsion stating that: "the long ovary of most orchids undergoes torsion (*resupination*) at the time of the opening of the flower, which causes the posterior side of the flower to assume

EXPLANATION OF THE ILLUSTRATION

GOODYERA PUBESCENS *R. Brown*. Plant approximately natural size with flowering and fruiting racemes detached, the flowers and fruit slightly less than natural size. 1, flower much enlarged to show the perianth. 2, flower sectioned to show the relation of the labellum and column to the ovary, sepals and petals. 3, column drawn to show position of stigmas and anther. 4, pollinia. 5, a pollen tetrad. 6, the mature seed.

Drawn by BLANCHE AMES

GOODYERA *pubescens R. Br.*

an anterior position." In my use of the term I have ignored the mechanical means by which the position of the labellum may be effected and have employed *resupination* whenever the labellum is visually the lowermost segment of the orchid flower.

As far back as Christian Konrad Sprengel's time, one hundred and forty-five years ago, the relation of the labellum of the orchid to pollination was understood; indeed, Sprengel was one of the first naturalists to emphasize this by pictorial means. On the quaintly adorned title-page of his Das entdeckte Geheimnis der Natur im Bau und in der Befruchtung der Blumen published in Berlin in 1793, he introduced a flower of *Listera ovata* with an insect on the labellum, its head in contact with the pollinia. But why the labellum of the orchid should have developed adaxially and then should have become the lowermost perianth segment by a half-twist and by curvature of the ovary is a biological mystery surrounding the effects of symbiosis.

Perhaps this mystery is intensified by *Malaxis paludosa*, a species with the labellum constituting the uppermost member of the perianth. To the casual observer the labellum of *M. paludosa* appears to be quite normally placed and as yet uninfluenced by the forces that cause resupination. Charles Darwin, in his lighter studies,[1] examined the flowers of this orchid and found that the position of the labellum is remarkable because it has been "purposely acquired" as shown by the "ovary"[2] being

[1] In a letter to Sir J. D. Hooker, Darwin wrote in 1861: "What frightful trouble you have taken about Vanilla; you really must not take an atom more; for the orchids are more play than real work."

[2] From my observations made on herbarium specimens I am of the opinion that the so-called twist is confined to the pedicel. Colonel M. J. Godfery is also of this opinion and in a letter has informed me that "the ovary itself is not twisted and is scarcely longer than its twisted stalk."

spirally twisted. In other words, *M.paludosa* has boxed the compass with its labellum in what "nature-lovers" might regard as a definite effort to accommodate fickle insects or to attain constancy in pollination through selective modifications adapted to insects with a preference for a non-resupinate flower. Indeed the labellum is the uppermost segment of the perianth because of a twist of the pedicel through 360 degrees. With characteristic promptness Darwin seized on this peculiarity of the pedicel in *M. paludosa* to strengthen the argument for his theory of natural selection and he referred to it as follows: "in many Orchids the ovarium (but sometimes the foot-stalk) becomes for a period twisted, causing the labellum to assume the position of a lower petal, so that insects can easily visit the flower; but from slow changes in the form or position of the petals, or from new sorts of insects visiting the flowers, it might be advantageous to the plant that the labellum should resume its normal position on the upper side of the flower, as is actually the case with *Malaxis paludosa*, and some species of Catasetum, &c. This change, it is obvious, might be simply effected by the continued selection of varieties which had their ovaria less and less twisted; but if the plant only afforded varieties with the ovarium more twisted, the same end could be attained by the selection of such variations, until the flower was turned completely round on its axis. This seems to have actually occurred with *Malaxis paludosa*, for the labellum has acquired its present upward position by the ovarium being twisted twice as much as is usual." (The various Contrivances by which Orchids are fertilized by Insects, ed. 2, p. 284)

Malaxis paludosa
after Darwin

There is surely something physiologically significant in the position of the labellum. It does not seem to be a matter of indifference to a species whether or not the flowers are upside down; whether the labellum is adaxial rather than the lowermost member of the perianth. Just recently I repeated an experiment I have often tried and by means of a string and anchor bent the inflorescence of *Calopogon pulchellus* so that the tip was directed toward the ground. In this species the labellum is normally the uppermost member of the perianth. In about a week the flowers began to expand and in each one the labellum had assumed the position characteristic of the species. These flowers had adapted themselves promptly to an unusual situation and the labellum was the uppermost perianth segment although the raceme was inverted. In the flowers of *Habenaria lacera* the labellum is the lowermost segment of the perianth. If the inflorescence is forcibly inverted so that the apex is directed toward the ground, the flowers as they expand will exhibit varying degrees of resupination, some of them being in the position they would have occupied had the raceme been allowed to remain upright. *Goodyera pubescens* presents an unusually interesting study in connection with resupination. If plants with the lowermost flowers fully expanded are inverted, the ovaries of the remaining flowers will continue to twist and anthesis being imminent, will for the most part cause complete resupination even though no perceptible torsion was observable in the ovaries of the buds. If plants with very young buds are inverted, resupination is checked and the labellum remains adaxial throughout the raceme. (cf. plate on p. 157) If a raceme, intermediate between imminent anthesis and extreme juvenility, is inverted, the flowers may turn variously so that the inflorescence appears to be composed of flowers in every conceivable stage of resupination. It is as if at the mo-

EXPLANATION OF THE ILLUSTRATION

GOODYERA PUBESCENS *R. Brown.* Above, a forcibly inverted raceme (slightly enlarged) in which the flowers have retained their primitive position with the dorsal sepal adjacent to the subtending floral bract. The ovaries have developed at right angles to the rachis. This condition should be compared with the obliquity of the ovaries in a normal raceme. (cf. plate of *Goodyera pubescens* on p. 151)

Below, a portion of the raceme enlarged about three times natural size.

Drawn with the aid of the camera lucida, August 1938 by BLANCHE AMES

GOODYERA *pubescens R. Br.*

ment of anthesis some irreversible surge of power were beginning to operate to cause the ovaries to twist. If a raceme is inverted before this power begins to manifest itself, resupination is prevented. However, as my observations on Goodyera have been confined to just a few plants, I feel that this matter is in need of further study, although Ziegenspeck in Lebensgeschichte der Blütenpflanzen Mitteleuropas (1936) p. 81, states that according to recent experiments the prevention of resupination by means of the klinostat is successfully done with Orchis (Dactylorchis), Habenaria (Platanthera) and Goodyera, only if very young buds are used. It has been stated that in Stanhopea, a very remarkable genus of orchids occurring in the American tropics, the flowers of the pendulous inflorescence if held erect will completely twist in twenty-four hours and assume the position they would have occupied had the inflorescence been pendulous. In the tropics where epiphytic orchids are not infrequently forced into unusual situations when they grow, with the racemes pendent, on tree trunks or on the sides of rocks or cliffs, I have observed on several occasions that the flowers become adjusted to whatever situation they are in and the labellum assumes the position that is normal for the species. This is true also of compound racemes or panicles in which some of the branches are at right angles to the main flower-shoot. In this case the ovaries of the laterally placed flowers twist through 90 degrees. This is true also for the lateral flowers of those species which have both terminal and lateral racemes. In the prevalently dimorphic genus Catasetum and in the dimorphic genus Cycnoches, the male flowers are frequently borne in elongated, drooping racemes; those of Catasetum being resupinate, those of Cycnoches being non-resupinate. Furthermore, in Catasetum the female flowers are usually produced on erect peduncles and are strikingly non-

CYCNOCHES STELLIFERUM *Loddiges.* The terminal portion of a pendulous raceme of male flowers. (The complete raceme consisted of twenty-three flowers.) The labellum, with radiating processes, is uppermost in the fully expanded flower. Above the labellum the lateral sepals are shown. The curved structure seeming to originate from the base of the labellum is the elongated pendent column with the anther and pollinia at the free end.

Drawn, from a plant collected in Honduras, by BLANCHE AMES

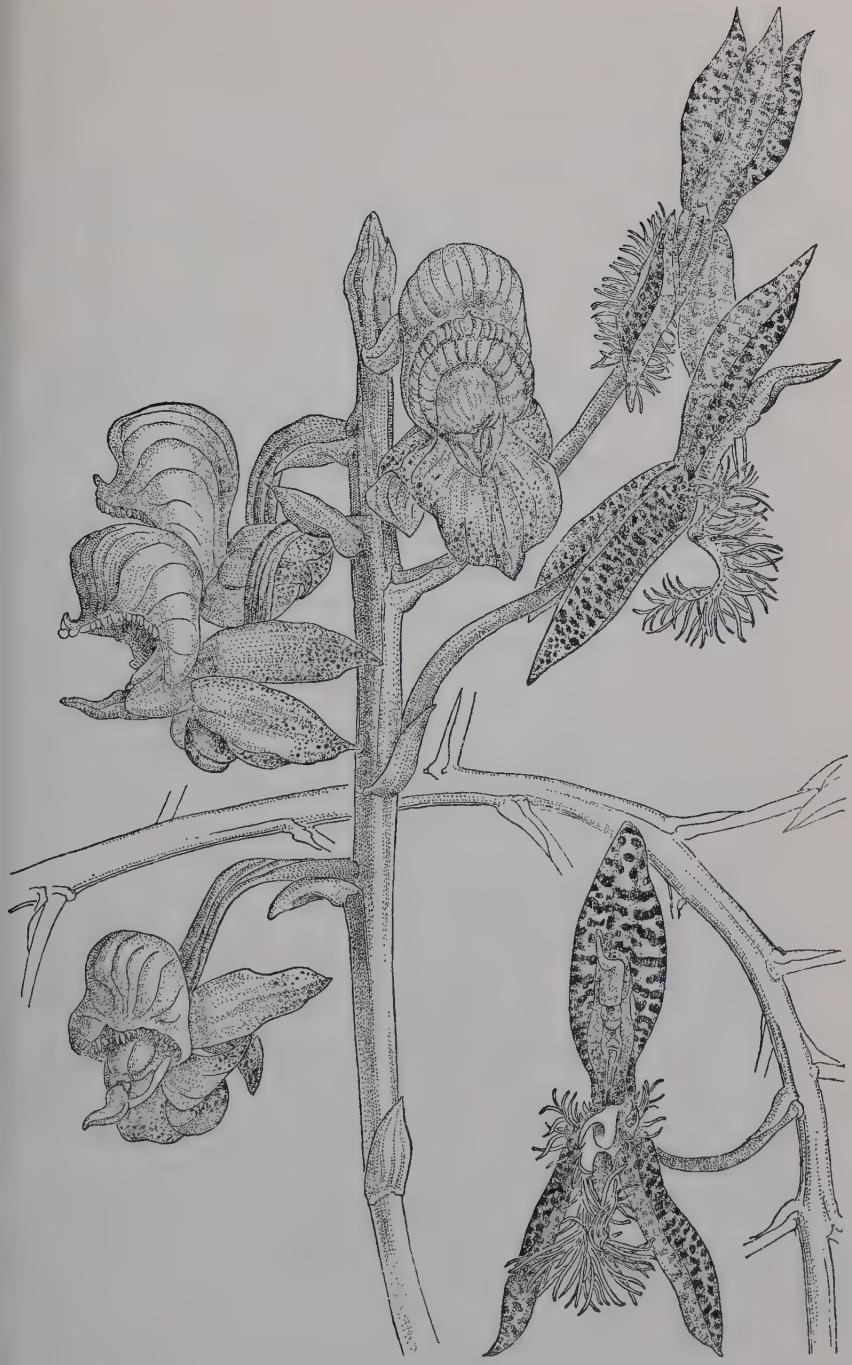
resupinate. When male and female flowers of certain species of Catasetum are produced simultaneously in a single raceme, the males are resupinate and the females non-resupinate. In Robert H. Schomburgk's famous paper published in the Transactions of the Linnean Society of London in 1837, the plate illustrating *Catasetum barbatum* shows both male and female flowers in the same raceme. (cf. illustration opposite p. 162) The males, with the fringed labellum lowermost; the fleshy females, with the deeply saccate or ventricose labellum uppermost, are just the reverse of what one would expect as a result of gravitational influence. They seem to indicate a selective response. This rare and abnormal association of male and female flowers in the same raceme throws light on the taxonomic significance of resupination in the Orchidaceae and in conjunction with the evidence of floral position as a physiological manifestation indicates that twisting of the ovaries is in no sense a symbol of specificity.

Before the true significance of flower-form and resupination in Catasetum was understood, there was a wilderness of error in the interpretation of generic and specific limits. John Lindley, in his treatment of the species now grouped under Catasetum (relying in part on resupination as a generic character), recognized three genera, namely, Catasetum, Monachanthus and Myanthus. In Myanthus the labellum, through resupination, constituted the lowermost segment of the perianth; in Catasetum the labellum was uppermost. In both concepts the column was typified by having a pair of antennae or cirrhi *(columna bicirrhosa). These genera proved to be composed of males.* In Monachanthus the labellum constituted the uppermost segment of the perianth and the column was different from that of Catasetum and Myanthus in lacking antennae or cirrhi *(columna mutica). The genus Monachanthus proved to be composed of females.*

EXPLANATION OF THE ILLUSTRATION

CATASETUM BARBATUM *Lindley*. Redrawn from a part of Schomburgk's plate in the Transactions of the Linnean Society 17 (1837) tab. 29, showing an *erect* peduncle bearing two male flowers, with the labellum barbate, and four female flowers with the labellum ventricose, the male flowers resupinate, the female flowers non-resupinate. In the lower right-hand corner a single male flower is shown resupinate although the raceme, composed of twenty-five male flowers, was *drooping* (in this flower the antennae or cirrhi may be seen above the hook-like callus at the base of the lip).

Before the dimorphic nature of this species was understood and before the sexes were found occurring simultaneously on a single plant, the female was called *Monachanthus viridis* and the male *Myanthus barbatus*. As early as 1826, John Lindley observed the occurrence of the two sexes of a species of Catasetum on the same raceme. He called the females "monsters" and let it go at that.

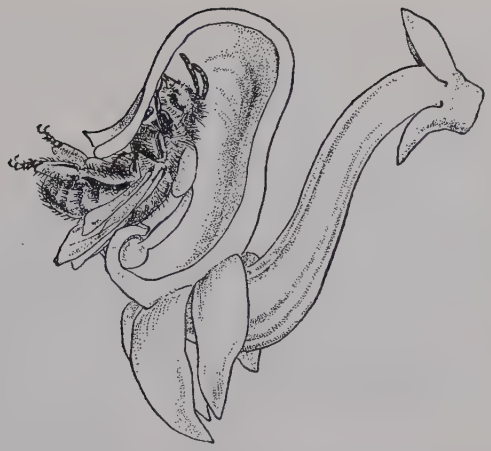


Charles Darwin was very much perplexed by the genera Catasetum, Monachanthus and Myanthus, because he was led to believe, mistakenly, that all three had been found on a single plant. Indeed down to this day, although R. Allen Rolfe explained the reason for Darwin's error (cf. Journ. Linn. Soc. Bot. 27 (1891) 206-225), we find an occasional recrudescence of this extraordinary belief. (cf. explanation of the illustration opposite the plate on p. 166.)

Notwithstanding the failure of resupination or torsion to designate genera in the Catasetum alliance, resupination is still used to differentiate between certain subtribes in the Neottiineae, the outstanding example being found in the Cranichideae which are separated from the Spirantheae and Physureae by having the labellum uppermost, that is the labellum is the posterior segment of the perianth. In this extremely puzzling aggregation there has been marked disagreement regarding the final resting-place of certain genera; Baskervillea, for example, having been referred to the Spirantheae in one system and to the Cranichideae in another. And Manniella, placed by Pfitzer in the Cranichideae, the subtribe with non-resupinate flowers, was made the type-genus of a new subtribe by Schlechter, distinguishable in part by the flowers being resupinate. In the Orchid Review 30 (1922) 3, Colonel M. J. Godfery directed attention to Georges Rouy's dependence on the ovaries in establishing subtribal differences between the Spirantheae and Physureae, the former having twisted ovaries, the latter untwisted ovaries (Flore de France 13 (1912) 209-210). Godfery argued that twisted and straight ovaries may occur in the same raceme of *Goodyera repens*, a member of the Physureae, and that therefore twisting of the ovary is of no value as a generic, still less as a subtribal character. A careful examination of the genera composing the

EXPLANATION OF THE ILLUSTRATION

CATASETUM MACROCARPUM *L.C.Rich. ex Kunth.* 1, a flower (labellum sectioned longitudinally) of the female, redrawn from H. Crüger's plate in the Journal of the Linnean Society 8, Bot. (1865) t. 9. The bee having gnawed the tissues on the anterior wall of the helmet-shaped labellum is shown leaving the flower. The pollen-masses from a male flower previously visited are being deposited on the stigmas. The male of *C.macrocarpum* (*C.tridentatum* of Darwin's writings, cf. fig. 2), is markedly unlike the female in the structure of the column. It differs from the male of *C.barbatum (Myanthus barbatus)* in the ventricose labellum and non-resupinate flowers. Schomburgk and Darwin believed that the female of both *C.macrocarpum* and *C.barbatum* represented a single species, namely *Monachanthus viridis*. It was this belief, formed through ignorance of the fact that the females of several species of Catasetum may be puzzlingly alike although the males are strikingly dissimilar, which contributed to the errors in Darwin's observations and conclusions. When a plant, supposedly *Monachanthus viridis* (in reality the female of *C.macrocarpum*), produced male flowers of *C.macrocarpum* (*C.tridentatum* of Schomburgk and Darwin) and when a plant of *C.barbatum (Myanthus barbatus)* produced typical male flowers, and females (supposedly *Monachanthus viridis*), simultaneously, in a single raceme, it was thought that two male forms (representing the genera Catasetum and Myanthus) were associated with a single female form (a Monachanthus) and it was assumed that *Catasetum tridentatum*, *Monachanthus viridis* and *Myanthus barbatus* were all referable to *Catasetum barbatum (Myanthus barbatus)*. To account for the difference between the males Darwin proposed that those of *Myanthus barbatus* should be regarded as being hermaphrodites. This was probably the crowning glory of biological and taxonomic misconception. 2, a male flower, redrawn from Hooker's Exotic Flora 2 (1825) t. 151.



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Cranichideae and Spirantheae makes one wonder if dependence on resupination or its opposite has not resulted in forced and unnatural alliances.

Harry Bolus in his treatment of South African orchids recognized as a section-character (§. Orthocarpa) the untwisted ovary in several species of Disa, a genus in which the flowers are preponderantly resupinate. Then he found in *Disa elegans* Reichb.f. (a species which he referred to §. Orthocarpa) that the "nearly posticous position" of the labellum is caused by a complete twist of the ovary. (Orchids of South Africa 1 (1896) t. 35) In this case the value of the presence or absence of ovarian torsion with regard to species of Disa seems to be severely weakened and of very questionable significance in the recognition of sections.

A more obvious peculiarity than twisting of the ovaries is torsion of the rachis when it twists either in a clockwise or counter-clockwise direction. Given equal weight with resupination as a diagnostic character, variation in the trend of spiral torsion would yield recognizable varieties in *Spiranthes gracilis* and *S.cernua* in which species the raceme twists one way or the other in different plants; but nobody, I think, would seriously employ this difference to establish subtribes, sections or species, even if it so happened that plants exhibiting one type or the other of spirality were to be found restricted to widely separated geographical regions.

In 1926, my colleague, Professor M.L.Fernald, reinstated from synonymy, as *Malaxis brachypoda*, an American orchid described as *Microstylis brachypoda* by Asa Gray in 1835. This concept is set apart from its ally, *Malaxis monophyllos* of Eurasia, because the flowers are resupinate. Undoubtedly in contrasting plants with resupinate and non-resupinate flowers a botanist accustomed to our native species with a pendent labellum

would, were he unmindful of the significance of resupination, conclude that it must be specifically distinct from an exotic though similar species with a non-resupinate, erect labellum. I would have no intention of taking exception to the proposals of Professor Fernald, if his conclusions were supported by all the evidence. He has reinstated *Microstylis brachypoda* to emphasize what he regards as a long overlooked difference between the American and Eurasian plants which have been prevalently referred to *Malaxis monophyllos*.[3] (cf. Rhodora 28 (1926) 176) In their vegetative and floral structure these plants are perplexingly alike. Professor Fernald's statement in Rhodora (l.c. p. 92) leaves no doubt as to what he regarded as the most important differentiating character. He wrote: "Most significant is the fact that the Eurasian plant has the flowers resupinate or up-side-down, so that the lip points up; while in the plants of eastern America the flowers are in normal position with drooping lip." It is quite evident that Professor Fernald uses the word resupinate incorrectly and in a sense very different from that understood by orchidologists and plant morphologists, and he has misinterpreted the behavior of the pedicel in the American plant although he used this structure in establishing a specific difference. The flowers of the Eurasian plant are not "upside-down" nor are the flowers of the American plant "normal" in having a "drooping lip". The American plant has a resupinate or abaxial perianth, whereas the perianth of the Eurasian plant is non-resupinate or adaxial.[4]

[3] In Rhodora 28 (1926) 92, Professor Fernald stated that I had ignored *Microstylis brachypoda* Gray in my Enumeration of the Orchids of the United States and Canada. In the Preface I made it clear that a complete synonymy would burden the text.

[4] James Edward Smith, in Smith and Sowerby's English Botany, used the term "*resupinata*" in describing the position of the "unpaired sepal" in the flower of *Malaxis paludosa*. He referred to this sepal as being "lowermost", assuming, also erroneously, that in the Orchidaceae the flowers are in their primitive position when the unpaired sepal is uppermost and the labellum lowermost. (cf. text cut on p. 154)

Perhaps, if it were not for the emphasis he places on the difference in the position of the labellum, and on supposed "complete geographic isolation", Professor Fernald would have been satisfied to have accepted an already proposed varietal concept.[5] Aside from the dissimilarity between *Malaxis monophyllos* var. *brachypoda* and *M. monophyllos* revealed by the position of the labellum, there may be slight, indeed elusive variations in the form of the flower-buds, relative size of the flowers and in the comparative length of the pedicels and mature capsules. Professor Fernald has attempted to reveal these variations as important differences by means of photographic evidence (Rhodora 35 (1933) tab. 253), but for this purpose his material from the Eurasian sources was doubtfully conclusive. For example, in the Gray Herbarium there is but a single specimen of the Eurasian *Malaxis monophyllos* with mature fruits. From this specimen Professor Fernald selected the capsules used in his illustration of contrasted structures and in making the

[5] Morris and Eames in Our Wild Orchids (1929) 358, used a varietal designation for the American plant and made the combination: *Malaxis monophyllos* Swartz var. *brachypoda* (Gray) Morris and Eames.

Professor Fernald would seem to criticize Morris and Eames because they used the name "White Adder's Mouth" for *Malaxis monophyllos* var. *brachypoda*. He admits that his familiarity with the Old World *M. monophyllos* and his conversance with folk-lore do not suffice to make it clear to him that this popular name applies to the European plant. As a "pseudonym" for the American plant with "greenish-yellow flowers" he regards the name as not descriptive (cf. Rhodora 35 (1933) 242). However, the name "White Adder's Mouth" has been used in American floras. It occurs in Britton and Brown's Illustrated Flora of the Northern United States and Canada; in Wild Flowers of New York by Homer D. House and elsewhere, and is not an innovation on the part of Morris and Eames. European botanists have described the flowers of the Eurasian plant as greenish, yellowish, etc. and have indicated this color in their illustrations. Therefore the flowers are similar in color to those of the American plant.

measurements used to establish a diagnostic point (Rhodora 35 (1933) tab. 253). In his description of the capsules and pedicels he gave comparative measurements. These are as follows for the Eurasian specimen: capsules 5–7 mm. long; pedicels 3–5 mm. long. (I have examined the specimen in question and have arrived at the following measurements: capsules 4–6 mm. long; pedicels 3–4.25 mm. long). For the American plant Professor Fernald gave the following measurements: capsules 3–5 mm. long; pedicels 1–2 mm. long. In my herbarium there is a specimen from Vermont from which the following measurements were taken: capsules 3–5.5 mm. long; pedicels 2–3.5 mm. long. The measurements from the Eurasian plant in the Gray Herbarium and from my Vermont specimen, being from only two examples, are of course inconsequential in diagnostic value, yet I think they are useful as they show overlapping of measurements although Professor Fernald indicates otherwise. However, the differentiating value of measurements in this case vanishes completely if we turn to a specimen in the herbarium of the New York Botanical Garden. This specimen was collected by P. Krylov in Siberia and includes a raceme with mature fruits, the capsules being 3.75–4.5 mm. long, the pedicels 2–2.5 mm. long. In the herbarium of the Field Museum of Natural History there is a fruiting specimen collected near Berlin in 1876 by Retzdorf with the capsules 3.5–4 mm. long and the pedicels 2.5–3 mm. long. In the United States National Herbarium there is a specimen with mature fruits collected by Hausser in 1885 in Pomerania with capsules 2.5–3.5 mm. long; pedicels 2–3 mm. long. Mr. Summerhayes has very kindly examined mature fruits of several specimens of the Eurasian plant preserved in the herbarium of the Royal Botanic Gardens at Kew. The minimum and maximum measurements are as follows:

capsules 2.7–4.8 mm. long; pedicels 2.4–4 mm. long.

Professor Fernald, in the explanation of his plate that illustrates the differences he would emphasize, refers to the capsules of the Eurasian Malaxis as having a projecting, shriveled perianth. He contrasts these with capsules from a Maine plant which have a reflexed perianth. At first glance one would regard the difference between the vestiges of the perianth as a substantial fruit-character, but the "projecting shriveled perianth" is due to the non-resupinate flowers which had the labellum directed away from the ovary. The "reflexed perianth" is simply the result of resupination, the labellum in this case having rested on the top of the ovary. This is, I think, clearly shown by the flowers in the plate on p. 177. So this difference stands or falls on the value attributed to resupination as a specific difference. Professor Fernald refers to the pedicels of the capsules in the Eurasian plants as being twisted and contrasts them with the pedicels of the American plants which he describes as being "straight". This difference is desperately difficult to accept because the pedicels are twisted in both the Eurasian and American representatives of *Malaxis monophyllos*; the only difference in the twist of the pedicels being that those of the American plants are twisted through 180 degrees and those of the Eurasian plants are twisted through 360 degrees, it being the additional twist which has returned the labellum to its primitive or non-resupinate position. In both the Eurasian and American representatives of *Malaxis monophyllos* a twisted pedicel is quite normal. The direction of the twisting, however, varies from flower to flower in the same raceme, and while some pedicels turn in a clockwise direction, others turn in a counter-clockwise direction. This peculiarity is clearly shown in the illustration of two capsules borne by a Vermont plant. Either Professor Fernald overlooked the twisted

The upper portion of a raceme showing the twisted, winged rachis and the twisted pedicels of the flowers. The bract of the lowermost flower has been removed. Drawn, much enlarged, from a specimen collected in Vermont by *Carl T. Ramsey*.

Two capsules from a plant collected in Vermont by *Carl T. Ramsey*, showing the twisted pedicels. (Capsules 5 mm. long; pedicels 3 mm. long. cf. p. 173, also p. 182.)

condition in his American material or else unwittingly used abnormal specimens in emphasizing a diagnostic point.

The value attributed to resupination when this peculiarity is associated with "complete geographic isolation" disappears when we find *Malaxis monophyllos* with non-resupinate flowers and its variant with resupinate flowers, growing in Japan. In my herbarium there are two specimens of *Malaxis monophyllos*, collected by Kenzo Shiota (No. 2222), on Mount Hakuso. Both specimens bear resupinate flowers and would pass without question for the New World plant if the geographical source were unknown. In the Gray Herbarium there is a specimen from Hokkaido, collected near Furebetsu, on which the flowers are non-resupinate. In all of these Japanese specimens the distinctive, thickened margin on the basal half of the labellum, a definite characteristic of the species, is present. This thickening, with some of the cells containing raphides, passes into short keels, one on each side of the disc, beneath each membranaceous, inrolled lateral lobe. This thickened margin is also well-developed in New World specimens of *Malaxis monophyllos* and is also distinguished by large cells containing raphides. The constancy of this thickened margin; the keels arising from it and the cells containing raphides are, in my estimation, strong characters aiding in the recognition of *Malaxis monophyllos*, and are of far greater diagnostic value as a specific guide than geographic isolation or differences in the length of the pedicels, capsules and flower-buds or differences in the position of the labellum; differences which are hardly reliable criteria for specific segregation in the Orchidaceae. (cf. plate on p. 177)

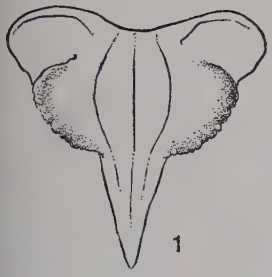
If the form of the labellum is studied in a series of specimens taken from the entire range of *Malaxis monophyllos*, it will be found that there are slight differences

EXPLANATION OF THE ILLUSTRATION

MALAXIS MONOPHYLLOS *(L.) Swartz* and var. BRACHYPODA *(A. Gray) Morris & Eames.* All of the figures are much enlarged. Figs. 1–7 represent lips taken from different plants and to aid in comparative studies they are represented in the same position. The basal lobes have been flattened out to reveal the outline. The magnification is similar throughout. 1, var. *brachypoda* from Newfoundland, 2 mm. long. 2, var. *brachypoda* from Vermont, 2.5 mm. long. 3, var. *brachypoda* from Japan, 2 mm. long. 4, *M. monophyllos* from Switzerland, 3 mm. long. 5, var. *brachypoda* from Vermont, 2 mm. long. 6, *M. monophyllos* from Japan, 2 mm. long. 7, *M. monophyllos* from China, 1.5 mm. long. 8, raphides found in the thickened margin and keels of the lip of *M. monophyllos* and var. *brachypoda*, much enlarged. 9, *M. monophyllos* from Siberia, lip 2 mm. long. 10, var. *brachypoda* from Vermont, lip 2.5 mm. long. 11, *M. monophyllos* from Pomerania, lip 2.5 mm. long.

Drawn with the aid of the camera lucida, figs. 2, 5, 8 and 10 from specimens preserved in alcohol; all other figures from dried specimens, August 1938 by

BLANCHE AMES



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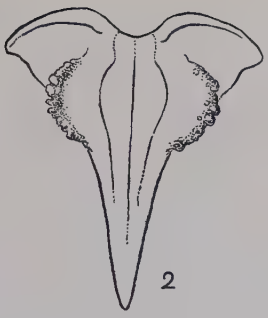

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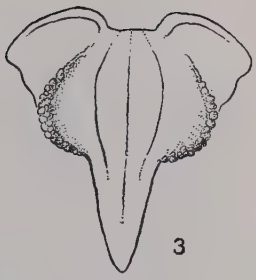

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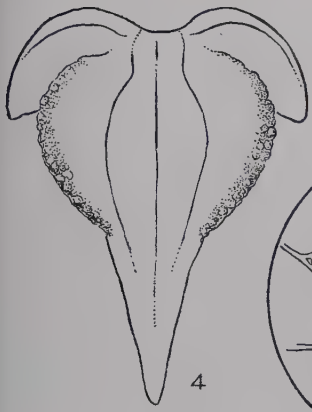

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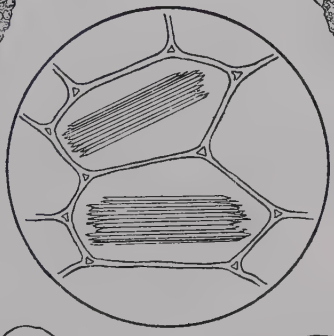

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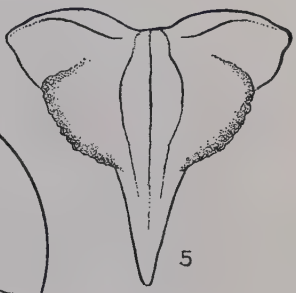

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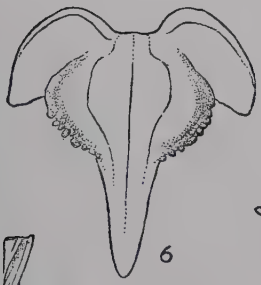

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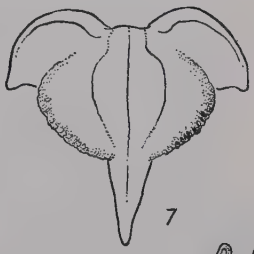

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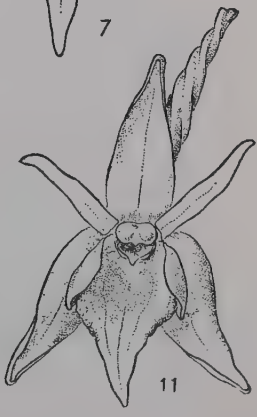

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between one specimen and another in the basal lobes or auricles. (cf. plate on p. 177) At first these differences are very perplexing. An attempt to utilize them in the recognition of two species, one American, the other Eurasian, would almost certainly necessitate the admission of several additional species separable by characters so slight and trivial that an attempt to make them clear by a description would be extremely difficult even if possible. Asa Gray originally thought there was a difference between the auricles or lateral lobes; those of the Eurasian plant being directed forward, those of the American plant being rounded and inrolled. The flowers of the Japanese specimen I have examined do not justify this view and between "triangular-hastate" and a distinctly three-lobed labellum, and between a short triangular terminal lobe and an elongated linear terminal lobe, every gradation may be traced. If the differences in the lobes are diacritical I think their value might be varietal at most. (cf. plate on p. 177)

All in all I believe the variation in the labellum and the differences emphasized by Professor Fernald would be regarded as inconsequential if they were to be observed among plants growing together in the same geographical area. Nevertheless, the position of the labellum is extraordinarily interesting, especially so, if leaning toward the conclusion that *M. brachypoda* and *M. monophyllos* are after all conspecific, we disregard slight dimensional dissimilarities in other parts of the flower: dissimilarities such as might originate in alliances that had been separated geographically for a long time. The position of the labellum in view of what has happened in *Malaxis paludosa* takes on fascinating significance. It arouses curiosity with regard to biological phenomena that have prevailed in widely separated regions where the influential association with unlike insects may have

caused the labellum to assume directly opposite positions. It arouses curiosity with regard to the taxonomic worth of resupination in the Orchidaceae. It aroused my curiosity very much as long ago as 1905, when I studied specimens of *Malaxis monophyllos* and *Microstylis brachypoda*, so-named, in the British Museum of Natural History. At that time I regarded resupination as being a weak character for the segregation of species in the Orchidaceae.[6]

Of course one might argue that resupination or its opposite is a strong and reliable diagnostic character because the orchid flower tends to become resupinate or otherwise when, through unusual circumstances, the perianth is so disposed that the labellum is forced away from its accustomed position. However, there is something here suggesting the strength of a sexual urge or a tropistic response rather than a deep-seated structural change. Indeed, there has not been any marked structural change in the perianth itself in *Malaxis monophyllos* or its variety. The change has occurred in the pedicel. Furthermore the instability of the resupinate condition as evinced by the evolutionary history of *Malaxis paludosa* should not be overlooked in the consideration of resupination in our taxonomic studies of the Orchidaceae, because in contemplating the significance of the twisted pedicel perhaps our imaginations are sufficiently vivid to conceive of a time when *Malaxis paludosa* had non-resupinate flowers; of a time when the flowers were resupinate; of a time, when by additional torsion of the pedicel, the flowers returned to their primitive position. But it would require

[6] Professor Fernald in Rhodora 28 (1926) 92 has assumed gratuitously that since Asa Gray described *Microstylis brachypoda* in 1835, students of the orchids have overlooked the difference between the plants of eastern America and the Old World, simply because they have not reinstated a species which subsequent to 1835 Gray himself reduced to synonymy under *Microstylis monophyllos*.

a very vivid imagination indeed to regard these states as specific, especially so should there be an untwisting action during the ripening of the capsule. If we turn once more to Darwin we find that he observed this phenomenon in *Malaxis paludosa* and referred to it as follows: "In all Orchids the labellum is properly directed upwards, but assumes its usual position on the lower side of the flower by the twisting of the ovarium; but in Malaxis the twisting has been carried so far that the flower occupies the position it would have held if the ovarium had not been at all twisted, and which the ripe ovarium afterwards assumes, by a process of gradual untwisting." (l.c.p.131) The untwisting of the pedicel or ovary during the ripening of the fruit rather belittles resupination as a specific character.

As I have previously stated, the flowers of the Eurasian *Malaxis monophyllos* have been turned completely round by a twist of 360 degrees in the pedicel. *M. monophyllos*, therefore, would seem to have had an evolutionary background comparable to that of *M.paludosa*, and at one stage in its history it had resupinate flowers similar in this respect to those of the American plant recognized as a distinct species by Professor Fernald. If, as Darwin suggested for *M.paludosa*, there is a process of untwisting as the capsule matures, it may well be that *M.monophyllos*, in so far as torsion is concerned, even now may become equivalent (if only for a brief time) to *M. monophyllos* var. *brachypoda*. In any event we should not overlook the fact that the labellum is adaxial in the bud in the American var. *brachypoda* and therefore nonresupinate and comparable in this respect before anthesis to the Eurasian *M. monophyllos*. It would certainly be stretching a point to argue that a single plant could be one species in the bud and quite another species in the expanded flower.

With regard to the untwisting of the pedicel as the fruit matures, I am unable to speak with assurance because I have not been sufficiently fortunate to have observed either *Malaxis paludosa* or the Eurasian *M. monophyllos* in the field. It would be hazardous to rely on the evidence furnished by herbarium specimens in attempting to decide this matter one way or the other. But it would be strange indeed if, regarding the untwisting of the capsule in *Malaxis paludosa*, Darwin made his statement gratuitously.

In the American plants of *M. monophyllos* var. *brachypoda* the pedicel of the flower is "straight" before anthesis. In other words, in the incipient stages of development the labellum is adaxial. As the buds swell the pedicels undergo gradual torsion and the perianth finally becomes resupinate with the labellum adjacent to the subtending floral bract. There is hardly any torsion in the ovary, however, traces of spirality being confined to the basal tissues. The twist in the pedicels persists as the capsule matures and the persistence of the twist is indicated by the labellum being the lowermost member of the shriveled perianth even when the capsules are ripe. I have not observed any tendency toward untwisting in the American plants of *M. monophyllos* var. *brachypoda* that I have studied in which torsion appears to be an irreversible condition, as is the case with *Corallorrhiza maculata* and other species in which torsion is more or less confined to the pedicels.

In *Goodyera pubescens*, untwisting of the ovaries is a conspicuous post-floral occurrence. Even before the last traces of white have faded from the withering sepals, the ovary will have untwisted 90 degrees or more and the labellum once again begins to incline toward the rachis of the raceme.

Resupination is a purely physiological phenomenon